



ECOSYSTEMS

Climatic niche shift after range expansion of *Eustachys* (Poaceae)

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Abstract: *Eustachys* presents lower diversity in the Old World than in the Neotropics and it occurs disjunctly between main tropical regions. This qualifies *Eustachys* as a good model to test whether lineages expand their niches during the process of range expansion. We performed ancestral range reconstruction, compared environmental spaces of the different geographic areas and assessed bioclimatic trait evolution. Ancestral range reconstruction indicated that most speciation in *Eustachys* occurred in the South America. Ancestral climatic niches of the New World are different from those of African and Australasia lineages. Our results show that *Eustachys* experienced niche expansion when it reached the New World. Evolutionary history of *Eustachys* illustrates how the range expansion promoted climatic niche shifts, which could drive unbalanced species richness of the genus among different tropical regions.

Key words: biogeography, disjunction, dispersal, ecological opportunities, grass.

INTRODUCTION

Dispersal allows taxa to reach new environmental conditions that are yet occupied in the source areas, promoting niche shifts (Simpson 1953, Yoder et al. 2010). Niche-based hypotheses suggest a positive relationship between available resources and species richness or between new niche conditions and diversification (Mahler et al. 2010, Wiens 2011, Yoder et al. 2010). Indeed, niche shifts can trigger events of diversification, as observed in a classical example of adaptive radiation among islands (Yoder et al. 2010). Recent evidences reinforce the role of climate or biome shifts for diversification in plant taxa (Cabral et al. 2021, Larridon et al. 2021, Villaverde et al. 2017, Wüest et al. 2015). However, whether climatic niche shifts are associated with range expansion is still a matter of debate (Pearman et al. 2008, Petitpierre et al. 2012).

Measuring volume of niche space is the first step to test these hypotheses because geographical areas with different ecological opportunities would exhibit greater niche space (Wiens 2011). Also, one might expect limited overlapping between niche volumes of geographical areas and divergent niche breadths among species from each different region, if it represents niche expansion. Due to advances in ecological niche modeling, several analytical tools can estimate niche total volumes, defined as environmental space (Qiao et al. 2016). Environmental space is a simplified representation of ecological niche, combining information on geographical occurrence and ecological variables (Soberón & Nakamura 2009).

Exploring how intercontinentally disjunct groups have dispersed and diversified allow us to understand how niche shifts are associated with movements of colonizing lineages.

Intercontinental disjunctions between tropical regions have been recorded for several taxa (Thorne 1972, Raven 1972). Advances in techniques for dating evolutionary histories have brought to light new proofs implying that these disjunctions were more likely established by long distance dispersal than vicariance (Christenhusz & Chase 2013, McLoughlin 2001). For families such as Poaceae, Gondwanan vicariance and recent long dispersal events explain intercontinental disjunctions of ancient and young lineages, respectively (Bouchenak-Khelladi et al. 2010). For example, molecular clock analysis indicated that Poaceae originated in Gondwana 96 Mya and its subfamily Chloridoideae most likely originated in Africa and/or Asia 30 Mya ago and later dispersed to the Americas (Bouchenak-Khelladi et al. 2010, Cotton et al. 2015, Peterson et al. 2010).

As a member of the Chloridoideae subfamily, *Eustachys* Desv. is a good model to test the hypothesis that range expansion can promote climatic niche shifts, since the genus present a intercontinental disjunct pattern (Bouchenak-Khelladi et al. 2010, Molina 1996). In addition, this monophyletic genus of the family Poaceae is represented by 15 species that have diversified in four main lineages, which are geographically structured suggesting that *Eustachys* expanded its range from Africa (2 spp) into Australasia (1 spp), and into New World, where most species (13 spp) of *Eustachys* occur (Molina 1996, Peterson et al. 2015). If *Eustachys* experienced a niche shift along its range expansion, the total volume of environmental space will differ between source and colonized areas. Also, lineages will show divergent scenarios of evolution in environmental space, such as significantly distinct niche breadths. Niche shift also could explain the unbalanced species richness of *Eustachys* between Africa, Australasia and the New World.

Here, we assess whether the range expansion of *Eustachys* is associated with evolution into a new realized climatic niche and into a greater environmental space. We hypothesize that range expansion of *Eustachys* promoted a shift in realized climatic niche in the evolutionary history of the genus and allowed it occupying climatic niches different from the source areas in Africa and Australasia. To address our main objective, we explore two questions: a) where is the most likely ancestral range of *Eustachys* in the New World?; and b) is range expansion of *Eustachys* to the New World associated with niche expansion?

MATERIALS AND METHODS

Phylogenetic analysis and divergence times

With the aim to infer the phylogenetic relationships within *Eustachys*, we sampled forty one species across genera of the tribe Eleusineae and used *Aeluropus lagopoides* (L.) Chiov. as the outgroup (Supplementary Material - Fig. S1). Sampling of *Eustachys* includes eleven species, which represents the entire morphological and biogeographical variation of the genus based on Peterson et al. 2015. We collected sequences of five DNA regions — one nuclear (ITS) and four plastid (*rpl32-trnL*, *ndhA*, *rps16-trnK*, *rps16*) — from data available in genbank (Benson et al. 2013). Accessions of genbank sequences and further information about vouchers are presented in Table S1. Automatic alignment of the sequences were carried out in Geneious v.7.1.7 (Kearse et al. 2012) using the MUSCLE algorithm (Edgar 2004). We performed manual adjustments when necessary, and concatenated the alignments of the five DNA regions using Geneious v.7.1.7. As a result, a database with 4,035 characters was produced.

We performed the Bayesian Inference (BI) and divergence time (DT) analysis in BEAST

v.1.10.4 (Suchard et al. 2018). The database was partitioned to analyze each region independently. For each partition, we selected a substitution model based on the results of an Akaike's Information Criterion analysis (Akaike 1998), executed in JModelstest v.2.1.6 (Darriba et al. 2012). The BI, DT and JModelTest were run through CIPRES Science Gateway (Miller et al. 2011). We applied the HKY-Gamma model for partitions represented by ITS and *rps16-trnL*, HKY-Inv for *rps16*, and JC-Gamma for *rpl32-trnL* and *ndhA*. Two independent Markov chains of 50,000,000 generations with trees being sampled every 1,000 generations were run. After the analyses, we discarded the first 10% of the generations in each Markov chain and used the remaining trees to access the maximum credibility tree and to calculate the values of posterior probability (PP) of each node.

The divergence time estimates were conducted with an uncorrelated relaxed clock model (Drummond et al. 2006), with a lognormal relaxed distribution rates, and a birth–death speciation model (Gernhard 2008) as a tree prior. The node age of tribe Eleusinae was secondary calibrated following Liu et al. (2011) in which a mean of 17.5 Mya. We applied a standard variation of 1.5, which corresponds to a variation of 15 to 20 Mya. Mean age for each clade of Eleusinae are presented in Table SII.

Ancestral range reconstruction

Information about geographical distribution of the species was collected from the Global Biodiversity Information System (GBIF). Only data that were georeferenced and identified by specialists were kept. Literature searches were carried out to remove areas in which species had been introduced or naturalized. Based on geographical range patterns identified for each species after the cleaning procedures in the dataset, we classified five areas of distribution:

A) Africa; B) Australasia; C) North America; D) Central America; and E) South America (Table SI). Species occurring in the Caribbean were included in the Central America classification.

We reconstructed the ancestral range of the main nodes in the *Eustachys* phylogeny, applying a bayesian analysis implemented in RASP v.4 (available at <http://mnh.scu.edu.cn/soft/blog/RASP/>). RASP tests which biogeographical model best fits the evolutionary history and geographical distributions of the studied group (Yu et al. 2015, 2020). We tested three biogeographic models: 1) S-DIVA (Statistical Dispersal-Vicariance Analysis) which optimizes an extinction, dispersal and vicariance matrix applying less “costs” to vicariance and calculates statistical support for each ancestral range in each node against several alternative scenarios (Yu et al. 2010); 2) S-DEC (Statistical Dispersal-Extinction-Cladogenesis) assumes that dispersal mediates range expansion and extinction mediates range contraction and calculates the probability of a event along a phylogeny branch according to the proportion of the same branch and the instantaneous transitions rates between geographic areas (Beaulieu et al. 2013); and 3) BAYAREA (Bayesian inference for discrete Areas) that calculates the probability of a biogeographic history using an “data-augmentation” approach in which a continuous-time Markov chain is used to simulate events of colonization and local extinction (Landis et al. 2013).

Because all the three biogeographical models include estimations of uncertainty, we used 1,000 trees randomly selected from a dataset of combined Markov Chains of dating analysis with 10,000 phylogenetic trees to explore which biogeographical model best explained the evolutionary history of *Eustachys*. We tested the three models implemented in RASP in two independent scenarios. First, we reconstructed the ancestral range without any restriction of

connections among the geographical areas. Second, we applied restrictions to connections among Australasia, North America and Central America, and between North America and South America. In both scenarios, we ran one analysis setting the minimum number of areas allowed by nodes, and another analysis setting the maximum number of areas. Since the focus of our study is the genus *Eustachys*, to reconstruct the ancestral range and niche evolution (see Niche evolution and ecological divergence below), we pruned the consensus tree excluding the outgroup and the other genera of tribe Eleusinae using the ape package (Paradis et al. 2004) in R environment (R Core Team 2020).

Niche evolution and ecological divergence

To test evolution of realized climatic niches in *Eustachys* and environmental space divergence among the geographical areas, we used 19 bioclimatic variables available in WorldClim 2.1 (Fick & Hijmans 2017) after clipping the variables to the extent of *Eustachys* occurrence (-176.6W, 175.1E, -40.8S, 36.8N), and applying a Spearman correlation analysis (threshold 0.85) to select the most independent bioclimatic variables. The selected variables were: BIO1 (annual mean temperature), BIO2 (mean diurnal range temperature), BIO4 (temperature seasonality), BIO5 (max temperature of warmest month), BIO8 (mean temperature of wettest quarter), BIO12 (annual precipitation), BIO13 (precipitation of wettest month), and BIO15 (Precipitation Seasonality). We performed these analyses in the packages “ntbox” (Osorio-Olvera et al. 2020) and “raster” v3.3 implemented in R.

We used the occurrence data to extract climatic data of the eight bioclimatic variables and then run a principal component analysis to represent the environmental space occupied by species of *Eustachys* of each geographical area in 3D using the software NicheA 3.0 (Qiao et al.

2016). We estimated the volume of environmental space of each geographical area as a minimum convex polyhedron (MCP). Then, we calculated the pairwise overlap between each area as a ratio of x/y , where x is the intersection of two environmental spaces and y is the volume of the smaller polyhedron in the compared pairwise.

For measuring phylogenetic signals of realized climatic niche in *Eustachys*, we performed a phylogenetic reconstruction of ancestral climatic traits. Firstly, using the occurrence data, we extracted climatic data and calculated the mean values of each bioclimatic for each species. Then, we estimated the evolution of each bioclimatic variable assuming a Brownian evolutionary model (*sensu* Revell 2013). Blomberg’s K and Pagel’s λ values of phylogenetic signal were calculated for each bioclimatic variable using the “Phytools” package (Revell 2012) for R. We also calculated the niche breadth of bioclimatic variables that presented phylogenetic signals for each species of *Eustachys*. To identify statistical significant differences among niche breadth of each species, Kruskal-Wallis and post hoc Wilcoxon tests were performed. In the Wilcoxon test, the p -value was corrected by the Holm method.

Additionally, we performed an Age Overlap Correlation Analysis (AOC) (Fitzpatrick & Turelli 2006) implemented in the package phyloclim 1.5-1 (Heibl & Calenge 2013). In this analysis, we explored the null hypothesis of absence of niche overlap along the evolutionary history of *Eustachys*. AOC also describes changes in niche overlap along the time. We used both D and I statistics of niche overlap and performed a Monte Carlo resampling of 10.000 replicates (Fitzpatrick & Turelli 2006).

RESULTS

Ancestral range reconstruction indicated the S-DEC with restriction and three areas by node as the best model to explain the evolutionary history and patterns of geographical distribution in *Eustachys* (LnL = -21.37, AICw = 0.75, Table SIII). In this model, intercontinental dispersions are assumed to have greater “costs” than vicariance. Also, in this model the probable ancestral range in each node is assumed as only a combination of three areas. However, this model presented some inconsistencies with the age of 4.8 Mya of *Eustachys* (HPD95% = 6.6–3.4 Mya) recovered by molecular dating analysis.

The selected model showed that the ancestral ranges of all *Eustachys* probably covered Africa, Australasia and South America (Fig. 1; ABE = 81%). For the common ancestor of *Eustachys tenera* plus American lineages, the model indicated Australasia plus South America as the ancestral range (Fig. 1; BE = 100%).

According to the model, two vicariance events established the main patterns of continental disjunctions in *Eustachys*: the first segregated the African lineages from the other lineages (ABE->A|BE, PP = 0.81); and the second led to the lineages from Australasia plus the Americas (BE->B|E, PP = 0.61).

For the American lineages, the model identified South America as the most likely ancestral range (Fig. 1; E = 61%). Four dispersion events occurred from South to North America and three into South America. Five speciation events were identified in South America, and three in North America. These results point to intense evolutionary dynamics of *Eustachys* during the last 2.1 Mya (HPD95% = 1.2–2.9 Mya) in South America. See supplementary material for the complete age estimates for the genera of tribe Eleusinae (Fig. S1).

Ecological divergence analysis showed that South America presented the largest

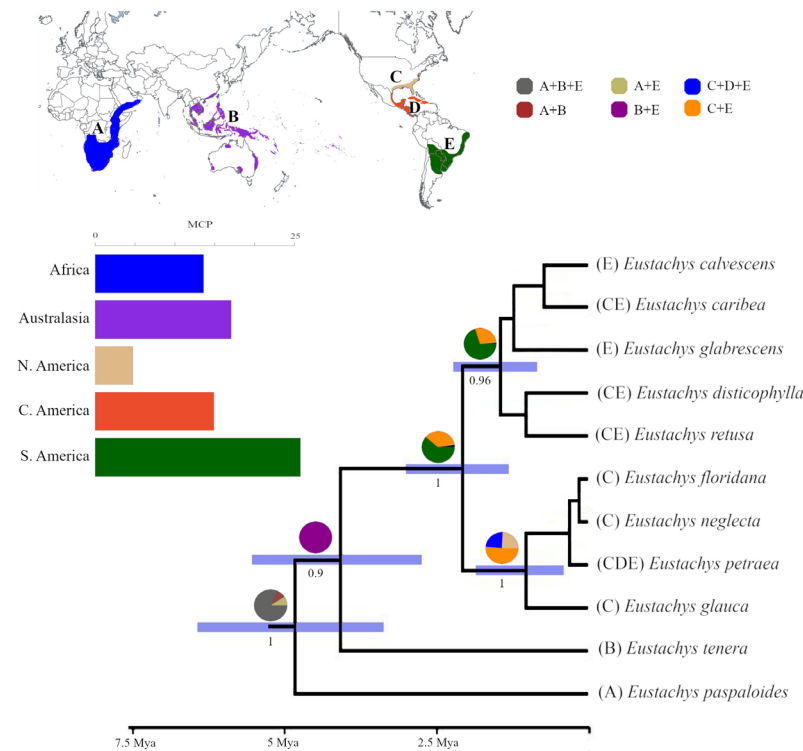


Figure 1. BEAST chronogram of Bayesian analysis of time divergence, geographical areas, ancestral range reconstruction, and volumes of the minimum convex polyhedron of the environmental space of each geographical area for *Eustachys*. Blue bars in phylogeny represent 95% confidence intervals. Posterior probability (PP) values are shown above branches only for the main clades with high support. The map shows the coded geographical areas used in the analysis. Pie chart shows the posterior probabilities of the ancestral ranges. The bar chart represents the minimum convex polyhedron (MCP) values of each geographical area. The colors used in the map, in the phylogeny and in the bar chart represent the geographical areas. Combinations of ancestral ranges found are presented in the above map. Area codes: A = Africa, B = Australasia, C = North America, D = Central America, and E = South America.

environmental space compared to other regions (MCP = 25.74). This indicates a higher volume of realized niche in South America when compared to other areas (Fig. 1). Overlaps between areas were often small (Table I). Pairwise comparisons of environmental spaces showed low values of overlap between South America and Australasia (Overlapping = 12.83), and South America and Africa (Overlapping = 11.66). However, the lowest values were found between North America and Australasia (Overlapping = 2.08), and North America and Africa (Overlapping = 0.57).

Four bioclimatic variables presented phylogenetic signals: BIO5 (max temperature of warmest month, $K=0.69$, $\log L=-17.94$, $\lambda=0.83$), BIO8 (mean temperature of wettest quarter, $K=0.56$, $\log L=-22.31$, $\lambda=0.99$), BIO12 (annual precipitation, $K=1.00$, $\log L=-76.11$, $\lambda=0.96$), and BIO13 (precipitation of wettest month, $K=0.88$, $\log L=-53.08$, $\lambda=0.980$). Reconstruction of the environmental variables showed a divergent pattern between the lineages, especially between the New World lineages and Paleotropical lineages (Fig. 2). For these variables, we found a negative slope higher than 0.5 in the AOC results (Fig. 3), indicating that recently diverged nodes are more similar than the early diverged nodes. However, all AOC results were inconclusive ($P > 0.05$), probably as an effect of the low number of internal nodes evaluated.

Niche breadth comparison among species confirmed the divergent patterns found in previous analysis (Fig. 4). Our results revealed

significant differences for all bioclimatic variables that presented phylogenetic signals (BIO 5: $X^2 = 1347.1$, $df = 963$, $P < 0.001$; BIO8: $X^2 = 1394$, $df = 996$, $P < 0.001$; BIO12: $X^2 = 1143.1$, $df = 744$, $P < 0.001$; BIO 13: $X^2 = 504.62$, $df = 261$, $P < 0.001$). *Eustachys paspaloides* has the most divergent niche breadths for all bioclimatic variables when compared with other lineages (Tables II and III), as the *E. tenera* diverges more from American lineages in the niche breadths of BIO5 and BIO 8 (Table III). In the temperature environmental spaces, North American lineages occupy smaller niche breadths while South American lineages present larger niche breadths (Fig. 4). In the precipitation environmental spaces, *E. tenera* presents the largest niche breadth and all American lineages occupy small niche breadths.

DISCUSSION

According to our results, *Eustachys* occupied a greater volume in the environmental space when it reached the New World, suggesting an expansion of its realized climatic niche. The realized climatic niches of *Eustachys* in the North, Central and South America are different from those of the African and Australasia lineages. In addition, South and North American lineages evolved in different environmental spaces in terms of each climatic variable. Evolutionary history of *Eustachys* illustrates how the range expansion promoted shifts in the realized climatic niche, which could drive

Table I. Pairwise overlapping values of environmental spaces between geographical areas of the distribution of *Eustachys*.

	Africa	Australasia	South America	North America
Australasia	6.26			
South America	11.66	12.83		
North America	0.57	2.08	3.34	
Central America	2.16	8.61	8.61	3.47

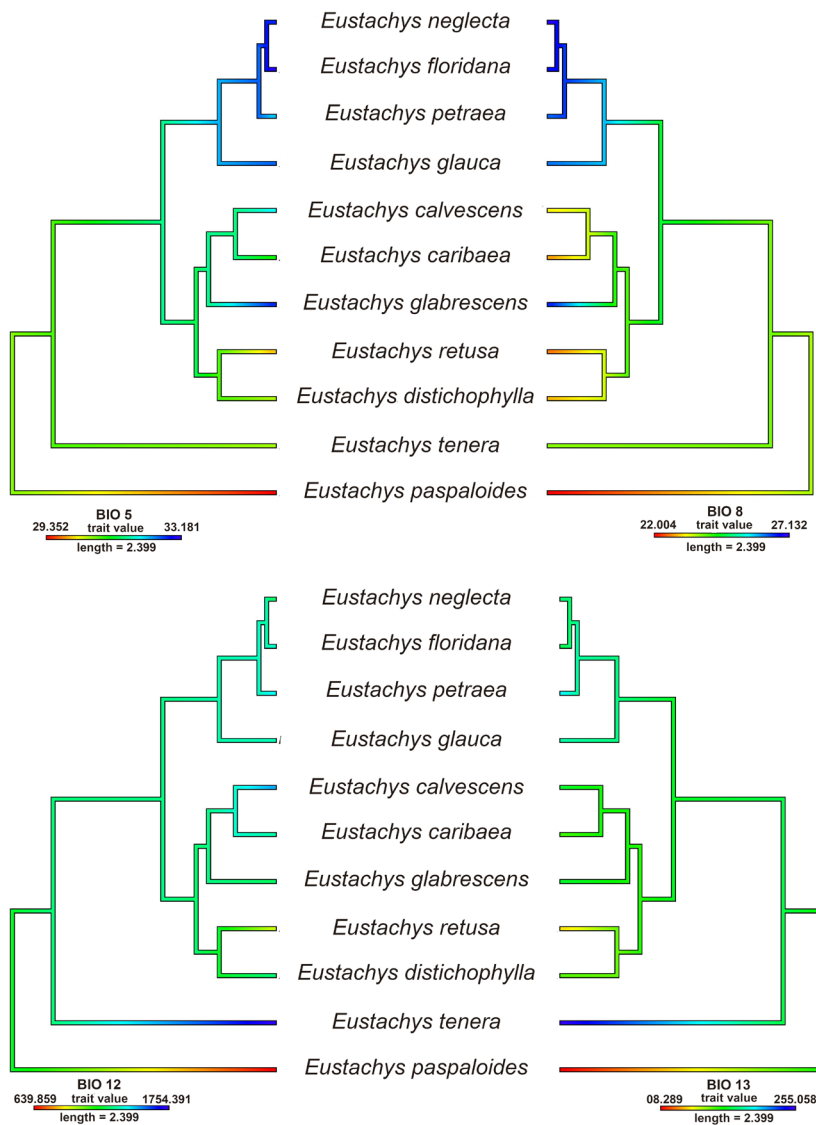


Figure 2. Representation of the evolution of *Eustachys* in each environmental variables that presented a phylogenetic signal. Bars represent the variation of each environmental variable. Bio5 = max temperature of warmest month, Bio8 = mean temperature of wettest quarter, Bio12 = annual precipitation, and Bio13 precipitation of wettest month.

unbalanced species richness among different tropical regions.

Ancestral range reconstruction points out that the vicariance process established the realized geographic pattern of distribution of species of *Eustachys*. However, there is an incongruence between the best model of geographic distribution recovered in ancestral range reconstruction and the evidence from dated phylogenies of Chloridoideae. According to Bouchenak-Khelladi et al. (2010), Cotton et al. (2015), and to our own results, Chloridoideae

diverged from its early ancestor 30 Mya and *Eustachys* ~4.8 Mya. This timeframe is incoherent with the vicariance by tectonic plate movements (Christenhusz & Chase 2013, Jokat et al. 2003, Raven 1972). At ~4.8 Mya, tectonic plate drift had positioned continents in their contemporary configuration (Jokat et al. 2003). Thus, we assume that long distance dispersal explains the geographical expansion of *Eustachys* from the Old World to the New World.

Geographical and evolutionary patterns found in *Eustachys* is one more example of the

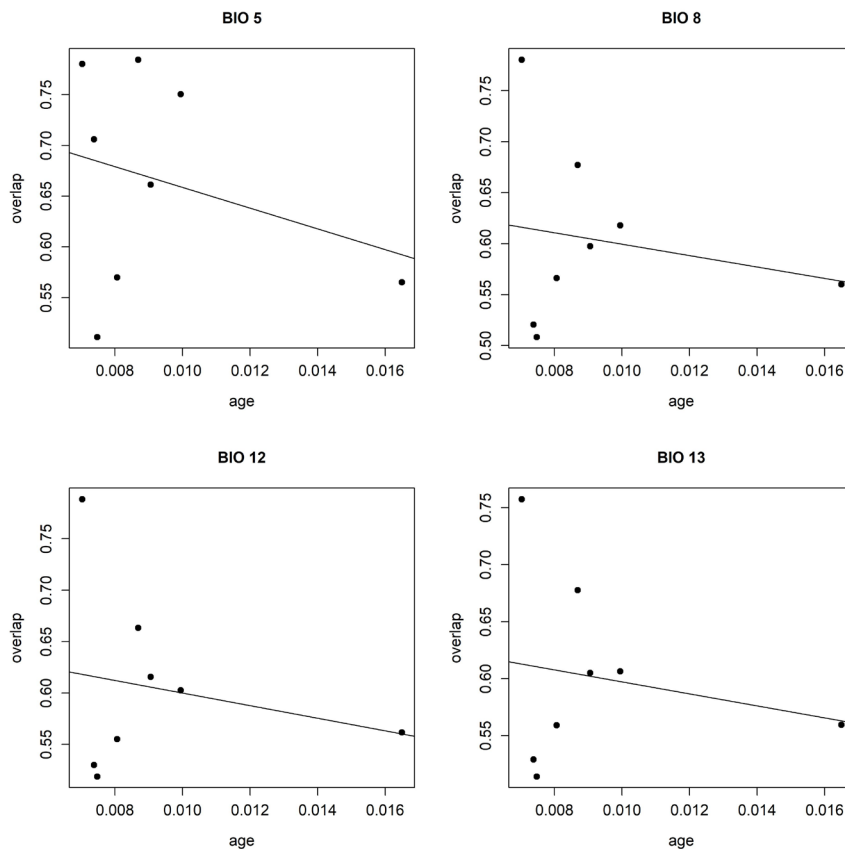


Figure 3. Results of Age Overlap Correlation analysis (AOC) of the bioclimatic variables that presented phylogenetic signals. Values represent both D and I metric of niche overlap in function of time of divergence of clades. Dots represent nodes in the phylogenetic tree. Line is the fitted regression. All AOC results were inconclusive ($P > 0.05$). Bio5 = max temperature of warmest month, Bio8 = mean temperature of wettest quarter, Bio12 = annual precipitation, and Bio13 precipitation of wettest month.

theory of intercontinental disjunctions (Thorne 1972). Such disjunctions have been explained mainly by vicariance events, but new evidence supports intercontinental disjunctions as a result of long distance dispersal more than vicariance (Christenhusz & Chase 2013, Raven 1972). In addition, long distance dispersal events from Africa to Australasia and from Australasia to South America have been recorded in several angiosperms species (Cuenca et al. 2008).

Evolutionary dynamics of *Eustachys* substantiates a niche expansion during the colonization of the New World, which could explain the high diversity of the genus in South and North America (Molina 1996). Indeed, we found that *Eustachys* experienced most of its diversification events in the New World and the speciation in South America was accompanied by the expansion into a greater environmental

space and by differentiation of realized niche. The volume of environmental space was relatively higher in South America compared to all other regions and the environmental spaces of Central and North America diverged from those of Australasia and Africa. We also found a general trend of older lineages present less overlap than younger lineages in AOC analysis. Expanding and differentiating environmental spaces of *Eustachys* agree with the expected effects of increasing ecological opportunities and niche shifts (Wiens 2011).

Evidences support that regions climatically stable and limited in niche breadth can trigger higher diversification (MacArthur 1972). In our study, we detected an opposite pattern. The region where *Eustachys* presents greater rates of speciation also possesses greater niche volume and hosts species with larger niche

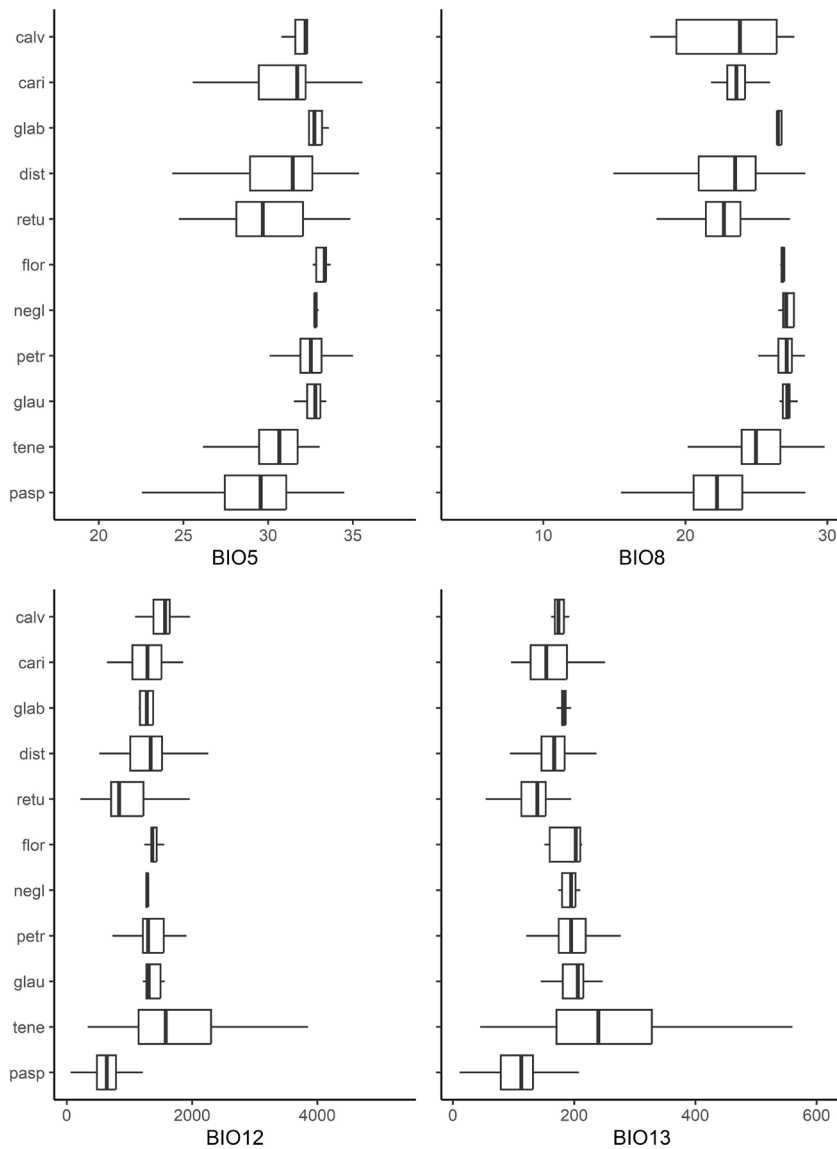


Figure 4. Representation of niche breadth of each species in the environmental spaces of the bioclimatic variables with phylogenetic signals. Outliers were omitted in the graph. Bio5 = max temperature of warmest month, Bio8 = mean temperature of wettest quarter, Bio12 = annual precipitation, and Bio13 precipitation of wettest month. Abbreviated names of species of *Eustachys*. pasp: *E. paspaloides*; tene: *E. tenera*; glau: *E. glauca*; petr: *E. petraea*; negl: *E. neglecta*; flor: *E. floridana*; retu: *E. retusa*; dist: *E. distichophylla*; glab: *E. glabrescens*; cari: *E. caribea*; calv: *E. calvescens*.

breadths in the temperature environmental spaces. However, our AOC results indicate that niche is not the only force acting in diversification of *Eustachys*. In grass genera, diversification can have several drivers, such as polyploidy and hybridization (Liu et al. 2011). Thus, one would expect that other forces previously documented for Poaceae could act conjointly with niche expansion in the diversification of *Eustachys*. Nevertheless, differences in niche volume among areas, differences of extension of niche breadth among species and niche expansion

potentially explain the imbalance in the number of species of *Eustachys* among regions.

Several tropical groups have higher numbers of species in the Neotropics than in any other tropical region. For example, the main lineages of Protiae diversified more in the Neotropics than in the Old World (Fine et al. 2014); the *Ocotea* Aubl. complex increased its rate of speciation after being dispersed from the Old World to New World (Chanderbali et al. 2001); and several lineages of *Euphorbia* L. reached higher diversification after colonizing

Table II. Wilcoxon pairwise comparison of niche breadth of Bio5 (max temperature of warmest month, lower table) and Bio8 (mean temperature of wettest quarter, upper table) of each species of *Eustachys*. In the columns, names of species were abbreviated. Significance levels after applying a Holm correction: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, non significant. Abbreviated names of species of *Eustachys*. pasp: *E. paspaloides*; tene: *E. tenera*; glau: *E. glauca*; petr: *E. petraea*; negl: *E. neglecta*; flor: *E. floridana*; retu: *E. retusa*; dist: *E. distichophylla*; glab: *E. glabrescens*; cari: *E. caribea*; calv: *E. calvescens*.

	pasp	tene	glau	petr	negl	flor	retu	dist	glab	cari	calv
<i>E. paspaloides</i>		***	***	***	***	***	ns	***	*	*	ns
<i>E. tenera</i>	*		***	***	*	*	***	***	ns	**	ns
<i>E. glauca</i>	***	***		ns	ns	ns	***	***	ns	***	*
<i>E. petraea</i>	***	***	ns		ns	ns	***	***	ns	***	*
<i>E. neglecta</i>	***	**	ns	ns		ns	***	***	ns	***	ns
<i>E. floridana</i>	***	***	*	*	ns		***	***	ns	***	*
<i>E. retusa</i>	*	ns	***	***	**	***		ns	*	ns	ns
<i>E. distichophylla</i>	***	ns	***	***	*	***	*		*	ns	ns
<i>E. glabrescens</i>	ns	ns	ns	ns	ns	ns	ns	ns		ns	ns
<i>E. caribea</i>	***	ns	**	***	*	***	ns	ns	ns		ns
<i>E. calvescens</i>	***	ns	ns	ns	ns	*	*	ns	ns	ns	

Table III. Wilcoxon pairwise comparison of niche breadth of Bio12 (annual precipitation, lower table) and Bio13 (precipitation of wettest month, upper table) of each species of *Eustachys*. In the columns, names of species were abbreviated. Significance levels after applying a Holm correction: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, non significant. Abbreviated names of species of *Eustachys*. pasp: *E. paspaloides*; tene: *E. tenera*; glau: *E. glauca*; petr: *E. petraea*; negl: *E. neglecta*; flor: *E. floridana*; retu: *E. retusa*; dist: *E. distichophylla*; glab: *E. glabrescens*; cari: *E. caribea*; calv: *E. calvescens*.

	pasp	tene	glau	petr	negl	flor	retu	dist	glab	cari	calv
<i>E. paspaloides</i>		***	***	***	***	***	***	***	*	***	***
<i>E. tenera</i>	***		ns	ns	ns	ns	***	***	ns	**	ns
<i>E. glauca</i>	***	ns		ns	ns	ns	***	***	ns	***	ns
<i>E. petraea</i>	***	ns	ns		ns	ns	***	***	ns	***	ns
<i>E. neglecta</i>	***	ns	ns	ns		ns	***	ns	ns	ns	ns
<i>E. floridana</i>	***	ns	ns	ns	*		***	ns	ns	ns	ns
<i>E. retusa</i>	***	***	***	***	ns	***		***	ns	*	***
<i>E. distichophylla</i>	***	*	ns	ns	ns	ns	***		ns	ns	ns
<i>E. glabrescens</i>	*	ns	ns	ns	ns	ns	ns	ns		ns	ns
<i>E. caribea</i>	***	ns	ns	ns	ns	ns	***	ns	ns		ns
<i>E. calvescens</i>	***	ns	ns	ns	ns	ns	***	ns	ns	ns	

the Neotropics (Riina et al. 2013). Other ecologically dominant groups in Neotropical ecosystems present the same pattern of higher diversification in the Neotropics (Pennington &

Dick 2004). Moreover, some lineages remain less diversified after colonizing the Old World, such as *Dalechampia* Plum. ex L. (Armbruster 1994) and *Rhypsalis* Gaertn. (Calvente et al. 2011).

Eustachys also expanded its range to new latitudinal limits along its evolutionary history. This expansion is associated with events of speciation in North America, where the smallest and most differentiated environmental space is found. Jansson et al. (2013) found that latitudinal transitions are frequent in tropical lineages and predominates over the presumed tropical conservatism, indicating that tropical lineages have few difficulties in colonizing new habitats. *Eustachys* adds one more example to the body of this hypothesis because its evolutionary history illustrates transitions to new environmental conditions.

We are aware that limitations in the dataset of climatic niches impose cautions for interpreting our results on niche reconstruction. Unfortunately, no dataset with climatic information of the last 5 or 10 Mya is available. Despite that, our dated phylogeny allows us to infer that the diversification of *Eustachys* happened during a period of intense environmental change in South America (Ehlers & Poulsen 2009). Driven mainly by Andean orogeny and climate changes, the last 5 Mya in South America recorded an intensification in climate changes, local tectonic pulses along the eastern coast, changes in watercourses, redirection of drainage systems, intense biotic interchange and marine transgressions (Antonelli & Sanmartín 2011, Antonelli et al. 2018, Cody et al. 2010). These events acting synergistically made the Neotropical region a land of evolutionary opportunities for *Eustachys*.

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SUPPLEMENTARY MATERIAL

Figure S1. Tables SI, SII, SIII.

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Paiva, Amorim and Maciel idealized the project, the analytical design and collected the data. Paiva and Amorim performed the phylogenetic and dating analyses. Paiva and Maciel performed all the niche analyses. Albuquerque conducted the critical review of the manuscripts and analysed the results. All the authors contributed equally to writing and revising the manuscript and its multiple versions.

